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On the Vegetation Types of Norwegian Conifer Forests in Relation to the Chemical Properties of the Humus Layer

Vegetasjonstyper i norske barskoger i forhold til humuslagets kjemiske egenskaper

Introduction

One of the chief aims of plant sociology is to produce a rational classification system of vegetation. Vegetation is highly variable in time and space, therefore some system is necessary to bring order into the often bewildering variation observed.

There is considerable controversy and discussion about methods of vegetation classification. One method is to use a classification procedure analogous to that used in taxonomy where individuals are classified in species, genera, families, orders etc. This method is used by the Zürich-Montpellier school as well as other schools which differ in their view about the characters likely to be most useful in vegetation classification. Thus the Zürich-Montpellier school emphasize the importance of characteristic species, while e.g. Scandinavian plant sociologists emphasize other vegetational characters such as species dominance. During recent times there has been an increasing mutual understanding between the different schools employing a classical classification procedure in vegetation study.

Other plant sociologists, especially in England and America, think that vegetation types grade imperceptibly into one another. In this situation a classical classification system may lead to serious distortion of facts. They use instead methods of ordination along gradients using numerical methods for identifying the gradients. They use methods more akin to those used in numerical classification in taxonomy.

In practical forestry, systems of forest types have long been in use. In Scandinavia the classification system of CAJANDER (1909) has been very important, while in Central Europe the classification systems are based upon the principles and methods of modern plant sociology.

Vegetation depends upon ecological factors. If a rational classification system is obtained, it is to be expected that the classification also contains information about ecological factors. It is the task of ecological plant sociology to identify the ecological differences between the vegetation types. In this way plant sociology becomes an important tool in the analysis of interrelations between vegetation and environmental (and historical) factors. This study is an attempt to identify ecological differences between vegetation types identified and defined by plant sociological classification methods.

Observations in Romedal, Hedmark, Norway

For two years, 1963 and 1965, a field course in forest ecology for forestry students has been given in the Romedal Almenning forest in Hedmark. The group of students were divided in small parties. Each party described the vegetation in plots of four different forest types by means of standard methods in plant sociology. Then a pit in each plot was dug, the soil profile described and samples taken to a field laboratory where soil data such as pH, loss in ignition, base saturation and cation exchange capacity, soil texture of C layer etc. were determined. The results were brought together in a table with both vegetational and soils data, one table for each type. The types used were a) a tall herb spruce type, b) an eutrophic low-herb spruce type, c) an oligotrophic *Vaccinium myrtillus* spruce type without eutrophic indicators and d) a pine type. From the tables the systematic vegetational differences as well as the associated differences in soils become apparent. Thus the soil in the tall herb type is invariably a brown earth, in the low-herb spruce type a weak podsol or a type intermediate between a podsol and brown earth (semipodsol). In the oligotrophic spruce and in the pine types the soil profile is normally a well developed iron podsol. This series is well known to be associated with the soil parent material and the water movements in the soils. Parent material from sediments rich in Ca as well as basic igneous rocks in localities where leaching is not too intense tend to produce tall herb vegetation types with brown earth while parent material from acid roks on well-drained sites tend to produce oligotrophic spruce and pine forests with podsols. This series is also well known to be associated with differences in forest productivity (see LÅG, 1959).

While clear differences in the chemical properties of the soils between the different spruce forests could be observed, the difference in soils between the oligotrophic spruce and the pine type was slight. This is surprising in view of the clear differences in vegetation between the two types. In the sociological classification these two types are placed in different alliances or even orders. There are many differential and some characteristic species and the division line is easy to observe in the field. One would expect such an important difference in vegetation to be associated with an equally important difference in environment. The field observations suggest that the difference hardly can be ascribed to climatic factors since both types can be found close together with no clear difference in preference for slope or aspect. It is a challenge to find out which environmental factor(s) is responsible for the difference between the two types.

In this situation the paper by HOLMEN (1964) appeared. He studied the content of plant nutrients in different peat types in the mire Jägaremossen in

Uppland, Sweden. By comparison of a purely ombrotrophic peat with a minerotrophic peat formed under an oligotrophic mire vegetation he found that the amount of total nitrogen differed radically between the types (see HOLMEN 1964, fig. 57 p. 164). In the ombrotrophic peat the total nitrogen was about 1 % while in the minerotrophic peat the content was 1.5 % higher. The difference in nitrogen was associated with a slight difference in available calcium.

Since many of the typical species of the pine forests also are capable of growing in ombrotrophic bogs while the typical species of the spruce forests are restricted to minerotrophic mires (fens) the suggestion was near at hand

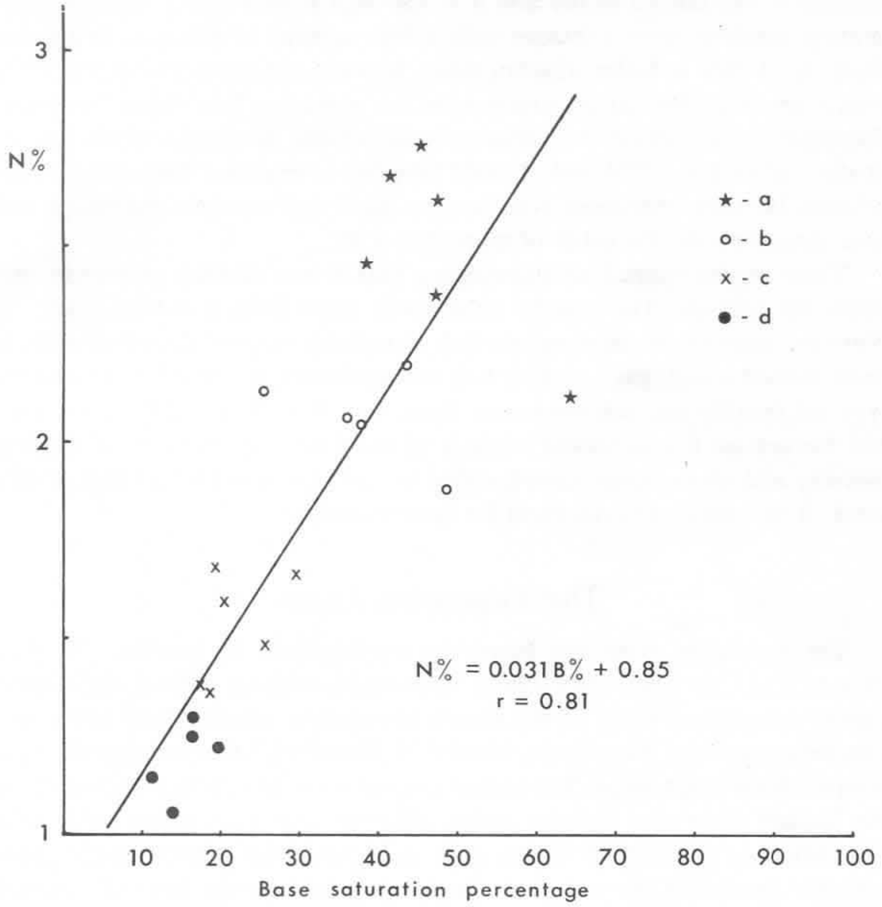

Fig. 1. Total nitrogen in per cent of loss ignition plotted against base saturation per cent for humus samples from Romedal Almenning, Hedmark. a) a tall herb spruce type, b) an eutrophic low-herb spruce type, c) an oligotrophic Vaccinium myrtillus spruce type and d) a pine type. Futher explanation in text.

that there might be a difference in nitrogen content of the humus between spruce and pine forest types. For this reason the humus samples from 1965 were analyzed for nitrogen.

In fig. 1 the total nitrogen taken as per cent of loss on ignition is plotted against base saturation per cent with different symbols for each of the forest types. There are significant differences in nitrogen content of the humus between all the four types and this factor discriminates between the spruce and the pine types. There is also a highly significant correlation between nitrogen content and base saturation. The difference between the types in terms of base saturation was known before and it is also well known that a high base saturation tends to give a humus with a high content of nitrogen. It appears from fig. 1 that a better discrimination between the types is obtained if the points are projected on an axis parallel the regression line. When this transformation is performed the variance ratio between groups to within groups comes out to $F = 55.4$ with 4 and 17 degrees of freedom. This shows a correlation between vegetation type on one hand and nitrogen percentage and base saturation on the other of more than 0.99.

These results seemed so encouraging that it was decided to expand and refine the analysis. The samples used above come from a restricted area of Norway. Since the vegetational analysis were made as part of student work, a more refined sociological analysis was not attempted. Especially the low-herb type indubitably was heterogeneous. Since one of us (J. K.-L) for some time has worked on a sociological analysis of the forest communities of Eastern Norway and since humus samples already had been collected as part of this work, it was decided to use them for further analysis.

The Vegetation Types

The vegetation types are based on investigations in Southern Norway (KIELLAND-LUND 1962, 1965, 1967). The communities are defined and named according to the methods of the Zürich-Montpellier school. Many of the soil samples come from Skrukkulia, Hurdal in Akershus, but supplemented with samples from other areas. The vegetation system is hierarchical with class as the highest unit, then follows order, alliances and associations with subassociation as the unit of lowest rank used here. The differential and characteristic species of the units have been recognized on the basis of regional studies in South Norway, with respect to the higher units also analytical data published from other areas in Europe have been utilized. (See table 1.)

Table 1. *Synoptic table, based on constancies (I—V), of the pine and spruce vegetation types.*

Type	1	2	3	4	5	6	7	8
	Vu–	Cl–	Ba–	Va–	Eu–	Eu–	Me–	Me–
					Pc	Pc	Pc	Pc
	Pn	Pn	Pn	Pn	My	Dr	ty	At
Samples	6	7	9	4	10	10	10	10
Class *Vaccinio-Piceetea:*								
Ch: *Pleurozium schreberi*	V	V	V	4	V	V	V	V
Vaccinium vitis-idaea	V	V	V	4	V	V	IV	V
,, *myrtillus*	IV	III	V	4	V	V	V	IV
Hylocomium splendens	I	II	V	3	V	V	V	V
Barbilophozia lycopodioides	.	I	V	2	V	V	V	V
Linnaea borealis	.	.	III	3	V	V	V	V
D: *Dicranum scoparium*	II	III	V	2	V	V	V	V
Deschampsia flexuosa	.	.	V	4	V	V	V	III
Betula pubescens	V	I	IV	1	II	.	.	II
Melampyrum pratence	I	.	IV	2	III	.	I	II
Order *Cladonio-Vaccinietalia:*								
Ch: *Cladonia silvatica*	V	V	V	3	I	.	.	.
,, *rangiferina*	V	V	V	3	.	.	I	.
Pinus silvestris	V	V	II	2	.	.	.	.
Dicranium undulatum	V	V	.	.	.	.	.	I
Cetraria islandica	.	III	V	2	.	.	.	.
Sphagnum nemoreum	IV	III	III	.	.	.	.	.
Cladonia alpestris	I	V	III	1	.	.	.	.
Vaccinium uliginosum	V	.	IV	.	.	.	.	.
Cladonia cornuta	II	II	III	2	.	.	.	.
,, *crispata*	I	III	II	1	.	.	.	.
Empetrum hermaphroditum	I	I	V	1	.	.	.	.
D: *Cladonia chlorophaea*	V	V	III	4	I	.	I	.
Calluna vulgaris	V	V	III	1	.	.	.	.
Ptilidium ciliare	II	V	II	.	I	.	I	I
Cladonia deformis	III	III	IV	1	.	.	.	.
,, *coccifera coll.*	III	III	IV	1	.	.	.	.
,, *gracilis*	.	V	III	2	.	.	.	.
,, *cenotea*	I	III	II	2	.	.	.	.
Association *Vaccinio uliginosi-Pinetum:*								
Ch: *Empetrum nigrum*	IV	.	.	.	.	.	.	.
D: *Polytrichum strictum*	V	.	II	.	.	.	.	.
Rubus chamaemorus	V	.	.	.	.	.	.	.
Eriophorum vaginatum	V	.	.	.	.	.	.	.
Oxycoccus quadripetalus	V	.	.	.	.	.	.	.
Sphagnum magellanicum	V	.	.	.	.	.	.	.
,, *fuscum*	V	.	.	.	.	.	.	.
,, *parvifolium*	V	.	.	.	.	.	.	.
Webera cfr. *sphagnicola*	V	.	.	.	.	.	.	.
Andromeda polifolia	IV	.	.	.	.	.	.	.
Aulacomnium palustre	IV	.	.	.	.	.	.	.
Cephalozia spp.	IV	.	.	.	.	.	.	.
Calypogeia spp.	III	.	.	.	I	.	.	.
Mylia anomala	III	.	.	.	.	.	.	.

Table 1. *(Continued). Synoptic table, based on constancies (I—V), of the pine and spruce vegetation types.*

Type	1 Vu– Pn	2 Cl– Pn	3 Ba– Pn	4 Va– Pn	5 Eu– Pc My	6 Eu– Pc Dr	7 Me– Pc ty	8 Me– Pc At
Samples	6	7	9	4	10	10	10	10
Alliance *Phyllodoco-Vaccinion:*								
Ch: *Nephroma arcticum*	.	I	II	1	.	.	.	.
Peltigera aphthosa	.	I	II	1	.	.	.	.
Cladonia bellidiflora	.	I	II	.	.	.	.	.
D: *Webera nutans*	I	V	II	.	.	.	.	.
Cladonia uncialis	I	V	II	.	.	.	.	.
,, *squamosa*	I	III	II	.	.	.	.	
Association *Cladonio-Pinetum:*								
Ch: *Arctostaphylos uva-ursi*	.	III	I	.	.	.	.	.
Dicranum spurium	.	IV	.	.	.	.	.	.
,, *robustum*	.	II	I	I	.	.	.	.
Association *Barbilophozio-Pinetum:*								
Ch: *Dicranum fuscescens*	I	I	V	3	III	I	I	.
Orthocaulis floerkei	.	.	IV	1	I	II	I	.
,, *attenuatus*	I	.	IV	1	I	.	.	.
Alliance *Dicrano-Pinion:*								
Ch: *Lycopodium complanatum* ..	.	.	II	1	.	.	I	.
Order *Vaccinio-Piceetalia* and Alliance *Vaccinio-Piceion:*								
Ch: *Picea abies*	V	III	IV	3	V	V	V	V
,, ,, — tree layer...	.	I	III	2	V	V	V	IV
Dicranum majus	.	.	II	2	V	V	IV	IV
Trientalis europaea	.	.	II	.	IV	IV	II	V
Lycopodium annotinum	.	.	.	2	IV	IV	II	IV
Rhytidiadelphus calvescens .	.	.	.	.	II	III	II	V
Ramischia secunda	.	.	I	.	.	III	II	IV
Hylocomium umbratum	.	.	.	.	.	IV	.	IV
Plagiochila major	.	.	.	.	.	II	I	IV
Listera cordata	.	.	.	1	.	II	I	I
Moneses uniflora	.	.	.	.	.	I	.	IV
D: *Luzula pilosa*	.	.	II	1	IV	V	V	V
Sorbus aucuparia	.	.	II	.	V	IV	IV	III
Majanthemum bifolium ...	..	.	.	.	V	V	III	V
Oxalis acetosella	.	.	.	.	I	V	V	V
Dryopteris linnaeana	.	.	.	.	I	V	IV	IV
Hieracium Silvatica group .	.	.	.	.	.	III	V	V
Agrostis tenuis	.	.	.	.	.	III	IV	V
Anemone nemorosa	.	.	.	.	.	III	IV	IV
Brachythecium reflexum	.	.	.	.	.	III	II	IV
Association *Eu-Piceetum:*								
Ch: *Dryopteris dilatata*	.	.	.	.	I	III	.	II
Obtusifolium obtusum	.	.	.	.	I	I	I	II
Sphagnum girgensohnii	II	.	.	.	.	I	.	I
,, *quinquefarium* .	.	.	.	.	I	I	.	I
D: *Polytrichum formosum*	.	I	.	.	III	III	I	I

Table 1. *(Continued) Synoptic table, based on constancies (I—V), of the pine and spruce vegetation types.*

Type	1	2	3	4	5	6	7	8
	Vu–	Cl–	Ba–	Va–	Eu–	Eu–	Me–	Me–
					Pc	Pc	Pc	Pc
	Pn	Pn	Pn	Pn	My	Dr	ty	At
Samples	6	7	9	4	10	10	10	10
Association *Melico-Piceetum:*								
Ch: *Melampyrum silvaticum* ...	.	.	.	.	I	I	IV	IV
Carex digitata	.	.	.	.	.	.	IV	IV
Calamagrostis arundinacea .	.	.	.	1	.	I	IV	II
Rhytidiadelphus triquetrus ..	.	.	.	.	.	I	I	V
Rubus saxatilis	.	.	.	.	.	I	.	V
Melica nutans	.	.	.	.	.	.	II	III
Pyrola rotundifolia	.	.	.	.	.	.	.	IV
D: *Veronica officinalis*	.	.	.	.	.	.	V	V
Anthoxanthum odoratum ...	.	.	.	.	.	.	V	IV
Solidago virgaurea	.	.	I	.	.	I	I	IV
Viola riviniana	.	.	.	.	.	.	II	V
Fragaria vesca	.	.	.	.	.	.	I	V
Potentilla erecta	.	.	.	.	.	.	II	III
Veronica chamaedrys	.	.	.	.	.	.	I	IV
Poa nemoralis	.	.	.	.	.	.	I	III
Athyrium subassociation:								
D: *Geranium silvaticum*	.	.	.	.	.	.	I	V
Rhodobryum roseum	.	.	.	.	.	I	I	IV
Ranunculus acris	.	.	.	.	.	I	.	V
Deschampsia caespitosa ...	.	.	.	.	I	.	.	IV
Aconitum septentrionale	.	.	.	.	.	.	.	IV
Dryopteris phegopteris	.	.	.	.	.	.	.	IV
Athyrium filix-femina	.	.	.	.	.	.	.	III
Carex vaginata	.	.	.	.	.	.	.	III
Prunella vulgaris	.	.	.	.	.	.	.	III
Crepis paludosa	.	.	.	.	.	.	.	III
Paris quadrifolia	.	.	.	.	.	.	.	III
Hypericum maculatum	.	.	.	.	.	.	.	III
Filipendula ulmaria	.	.	.	.	.	.	.	III
Alnus incana	.	.	.	.	.	.	.	III
Other species (frequency ≧ III):								
Polytrichum juniperinum ..	.	I	III	1	I	.	I	I
Plagiothecium laetum	.	I	.	.	I	II	III	I
,, *denticulatum*.	.	.	.	.	I	II	.	III

The system obtained show some similarities with the system of CAJANDER (1909) and CAJANDER and ILVESSALO (1921), but the correspondence is better with the forest type system now used in the Norwegian forest survey proposed by MORK (1956). Indeed the conformity of the units is quite pronounced.

All plant communities described here belong to the class *Vaccinio-Piceetea* Br.-Bl. 1939 where most of the northern and boreal coniferous forests belong.

In the climax stage *Pinus silvestris* and *Picea abies* dominate. In the field layer chamaephytes and ericaceous species like *Vaccinium myrtillus*, *V. vitis-idaea* and *Linnaea borealis* are common. The moss layer is well developed with *Hylocomium splendens*, *Pleurozium schreberi*, *Ptilium crista-castrensis*, *Barbilophozia lycopodioides* etc.

The class is commonly divided into two groups. The first group comprises the strongly oligotrophic pine forest with an associated flora of xeromorphic species. The other group comprises the spruce forests which are less oligotrophic or eutrophic or even calcicolous with a more mesophytic flora. The spruce forests belong to the *Vaccinio-Piceion* Br.-Bl. 1939. However the pine forests are quite heterogenous and can at least be divided in two alliances, a more southern *Didrano-Pinion* Libbert 1933 with species like *Pyrola chlorantha*, *Lycopodium complanatum* and *Chimaphila umbellata*, and a more northern and low-mountain alliance the *Phyllodoco-Vaccinion* Nordh. 1936 with species like *Phyllodoce coerulea*, *Orthocaulis floerkei*, *Nephroma arcticum*, *Cladonia bellidiflora* and others. Together with the pine forests in bogs and oligotrophic wind heaths in the mountains, these communities form a fairly well circumscribed order which recently has been named *Cladonio-Vaccinietalia* Kielland-Lund 1967. The characteristic and differential species of the order and of the units of lower rank are given in table 1.

Within the pine forests, three groups of communities can be recognized. The first group comprises the association *Vaccinio uliginosi-Pinetum* Kleist 1929. This association is probably the most oligotrophic growing on fairly well drained, ombrogenous peat along bog edges etc. The vegetation consists of a mixture of dry-land pine forest species and bog species of the alliance *Sphagnion fusci* with species like *Vaccinium uliginosum*, *Eriophorum vaginatum*, *Rubus chamaemorus* and several *Sphagnum* species. *Empetrum nigrum* is perhaps a regional characteristic species of the association.

The second group comprises two associations which together are placed in the alliance *Phyllodoco-Vaccinion*. The first association is the *Barbilophozio-Pinetum lapponicae* Kielland-Lund 1967. This is a highland pine forest of cool and humid regions often represented as a mixed forest of northern pine *(Pinus silvestris* ssp. *lapponica)* and mountain birch. *(Betula pubescens* ssp. *tortuosa)*. Ericaceous species dominate the field layer, *Vaccinium uliginosum* on mineral soil is typical. Regional characteristic species of the association are the hepatics *Orthocaulis floerkei*, *O. attenuatus* and *Barbilophozia* cfr. *hatcheri*.

The second association is the *Cladonio-Pinetum boreale* (Cajander 1921) Kielland-Lund 1967. The pine-lichen forest is certainly the most common and widespread pine forest type in Fennoscandia on outwash gravel plains or on rocky ground in continental areas. On the gravel plains the pine forest is usually well stocked, while on rocky ground the forest is more open, often with dominant *Calluna*. Lichens always play a considerable part in the bottom layer. Probable regional characteristic species are *Arctostaphylos uva-ursi*, *Dicranum spurium* and *Monotropa hypopitys*.

The third group of pine forests are placed in the alliance *Dicrano-Pinion* Libbert 1933 s.str. with one association, the *Vaccinio-Pinetum boreale* Cajander 1921. This association is found in the lowlands of southern Fennoscandia on sandy plains with deeper and somewhat better soils than the *Cladonio-Pinetum*. In the well-stocked tree layer pine is dominant, generally with spruce codominant. The most prominent species in the field layer are *Vaccinium vitis-idaea* and *V. myrtillus*. In the bottom layer mosses are more common than lichens. Character species are *Pyrola chlorantha*, *Lycopodium complanatum* and *Chimaphila umbellata*.

This community is closely related to the *Myrtillus* spruce forests and the two types resemble each other in ecology and physiognomy. They often replace each other apparently in response to minor changes in soil conditions.

The spruce forests are placed in the order *Vaccinio-Piceetalia* s.str. with one alliance in the area, the *Vaccinio-Piceion*. Br.-Bl. 1938. The alliance comprises two different associations, the *Eu-Piceetum* (Cajander 1921) Kielland-Lund 1962 and the *Melico-Piceetum* (Cajander 1921) Kielland-Lund 1962. The *Melico-Piceetum* occurs on more calciferous soils in warmer localities than the *Eu-Piceetum*.

The association *Eu-Piceetum* is divided in two subassociations, the *Myrtillus* subassociation and the *Dryopteris* subassociation.

The *Eu-Piceetum Myrtillus* subassociation is the most common forest community in Fennoscandia occuring on medium productive upland soils. Spruce is the dominant tree, pine being more common in continental areas and after clear-cutting. In the poorly developed shrub layer *Sorbus aucuparia* is common, while *Vaccinium myrtillus* dominates the field layer entirely in more open stands. Good differential species against the pine forests are *Majanthemum bifolium*, *Trientalis europaea* and *Luzula pilosa*. The moss layer is well developed. The *Myrtillus* subassociation differs from the *Dryopteris* subassociation mainly by the absence of the eutrophic species of the *Dryopteris* subassociation.

The *Eu-Piceetum Dryopteris* subassociation is fairly common in valleys and mountain forests. It is found on richer soils than the *Myrtillus* subassociation, often on soils with sideways movement of ground water and contains some eutrophic species like *Anemone nemorosa*, *Oxalis acetosella* and *Dryopteris linnaeana*.

The *Melico-Piceetum* is a herb forest community with species like *Melampyrum silvaticum*, *Viola riviniana* and *Rhytidiadelphus triquetrus* as possible regional characteristic species. Some of its differential species like *Carex digitata*, *Poa nemoralis*, *Melica nutans* and *Anemone hepatica* are considered characteristic species of the broadleaved forests of Central Europe (class *Querco-Fagetea*) and may be termed transgressive character species of the *Melico-Piceetum*. A well-stocked spruce tree layer is typical with pine, *Betula verrucosa* and *Populus tremula* often in the pioneer stages. The typical subassociation has a distinctive southern distribution and in the valleys it grows on southern exposure while in northern exposure it is replaced by the *Eu-Piceetum Dryopteris* subassociation.

The *Melico-Piceetum Athyrium* subassociation may be termed the tall-herb spruce forest. It is a pure spruce forest with a luxuriant field layer with tall herbs, broadleaved grasses and ferns. Conspicuous differential species are *Aconitum septentrionale* and *Athyrium filix-femina*. The stands represented in table 1 belong to a variety influenced by grazing as shown by the presence of species like *Carex vaginata*, *Prunella vulgaris* and *Pyrola rotundifolia*, while species sensitive to grazing like *Mulgedium alpinum*, *Campanula latifolia* and *Milium effusum* are subordinate or lacking. The community is found in valley sides and bottoms with periodical seeping water (flush). On even more nutrient-rich sites tall herb communities are found with few or no trees, belonging to another vegetation class, the *Betulo-Adenostyletea*.

The vegetational system can be summarized thus with numbers and abbreviations used in the tables.

Class *Vaccinio-Piceetea.*	
Order *Cladonio-Vaccinietalia.*	
Alliance ?	
Association *Vaccinio uliginosi-Pinetum*	1. Vu-Pn.
Alliance *Phyllodoco-Vaccinion*	
Association *Barbilophozio-Pinetum*	2. Ba-Pn
Association *Cladonio-Pinetum boreale*	3. Cl-Pn
Alliance *Dicrano-Pinion* s.str.	
Association *Vaccinio-Pinetum boreale*	4. Va-Pn
Order *Vaccinio-Piceetalia s.str.*	
Alliance *Vaccinio-Piceion*	
Association *Eu-Piceetum*	
Myrtillus subassociation	5. Eu-Pc My
Dryopteris subassociation	6. Eu-Pc Dr
Association *Melico-Piceetum*	
Typical subassociation	7. Me-Pc ty
Athyrium subassociation	8. Me-Pc At

Table 2. *Sørensen indices of floristic community (in per cent) between the vegetation types. Upper right based on all species present in the stands analyzed, lower left based on species present with constancy III or more. Further explanation in text.*

Type	Pine forests *Cladonio-Vaccinietalia*				Spruce forests *Vaccinio-Piceetalia*			
	1 Vu–Pn	2 Cl–Pn	3 Ba–Pn	4 Va–Pn	5 Eu–Pc My	6 Eu–Pc Dr	7 Me–Pc ty	8 Me–Pc At
1 Vu–Pn		50,9	49,6	44,9	30,0	15,0	17,9	12,0
2 Cl–Pn	50,0		63,2	58,8	32,7	21,6	26,8	14,9
3 Ba–Pn	45,6	56,5		65,0	42,9	31,7	38,0	20,6
4 Va–Pn	32,0	52,2	70,6		47,7	35,8	41,4	20,9
5 Eu–Pc My	17,0	23,3	50,0	68,3		68,0	60,2	40,2
6 Eu–Pc Dr	14,5	19,6	35,7	49,0	73,9		68,3	53,0
7 Me–Pc ty	15,1	20,4	37,0	46,8	63,6	73,1		58,9
8 Me–Pc At	9,5	12,5	23,5	30,8	42,7	60,2	56,8	

To illustrate the floristic relationships between the vegetation types, indices of floristic community have been calculated based on the stands where soil samples also were taken for chemical analysis. The index used is that of SØRENSEN (1948) which actually is a variant of the index of JACCARD (1902) since they contain the same amount of information (DAHL 1956 p. 58). CURTIS (1959 p. 83) ascribes the index to CZEKANOWSKI (1913) but no mention of the index has been found in the Polish paper. The index is:

$$K_s = \frac{2c}{a + b}$$

where a is the number of species present in the first type, b is the number of species in the second type while c is the number of species shared between the types. A high index indicates close floristic similarity. Two different indices have been calculated and given in table 2. The indices on the upper right is based on all species present, the indices in the lower left are based on presence of species with constance of III or higher.

The difference between the pine and the spruce communities is evident, high index values occurring within the groups while between groups the indices are lower. Relatively high indices are present between the *Vaccinio-Pinetum* and the *Eu-Piceetum Myrtillus* subassociation, especially if only species with constancy III or higher are considered. In general the indices bear out the classification system.

Chemical Analysis

The air-dried samples from the A_0 or A_1 layers, one sample from each stand, were analyzed in the chemical laboratory of the Norwegian Forest Research Institute. The samples were pretreated by sieving through a 2 mm sive, whereby coarse roots, twigs etc. were removed. As all analysis data are on a dry matter basis, the water content was determined by drying the sample at 105°C. Loss on ignition was determined by heating the samples at 550°C and taken to represent the amount of humus.

Nitrogen was determined by a semi-micro Kjeldahl method after digestion with sulphuric acid using copper sulphate as a catalyst.

Cation exchange capacity and base saturation were determined by first leaching the sample with neutral 1 N ammonium acetate until no change in pH of the solution passing the sample could be observed. In the filtrate sodium and potassium were taken by flame photometry, calcium, magnesium and manganese by atomic absorption flame photometry. The base saturation deficit was determined by titrating an aliquot of the filtrate to pH 7 with 0.1 N NaOH, using an automatic titrator. The cation exchange capacity is the sum of base saturation deficit and the metallic cations expressed in milliequivalents per 100 g soil. The base saturation is the amount of metallic cations in per cent of the cation exchange capacity.

The results of the chemical analyses were first given a preliminary examination. In general the values for each element varied within a reasonable narrow field within types with two exceptions. On sample from a *Barbilophozio-Pinetum* and one from a *Vaccinio-Pinetum* were unusually rich in nitrogen and one of them also in calcium. The chemical analysis was repeated, but no analytical error could be found. The conditions of the stands were then studied. It was found that one of them was situated near a path where cattle from a farm use to go on their way to their grazing areas. The other was situated near an often visited outlook. It was concluded that these two samples may have been contaminated by droppings from cattle or man and therefore could be excluded from the material.

Statistical Analysis

1. *Choice of variables*

From the chemical analysis a set of data for each soil sample is obtained. These data are not all independent e.g. cation exchange capacity is calculated from the sum of metallic cations present and the base saturation deficit. The use of functionally dependent variables can cause trouble in statistical analysis. It is also advantageous to use only a restricted number of variables since the computational load increases sharply with the number of variables included.

It is a great advantage in statistical work if the analysis can be based on normally distributed variables. If the observations suggest non-normal variables, a suitable transformation may often transfer non-normal variables to normal. Since concentrations of elements essentially are non-negative and the relative standard error (mean divided by standard error) can be high, it follows that such variables cannot be treated as normal.

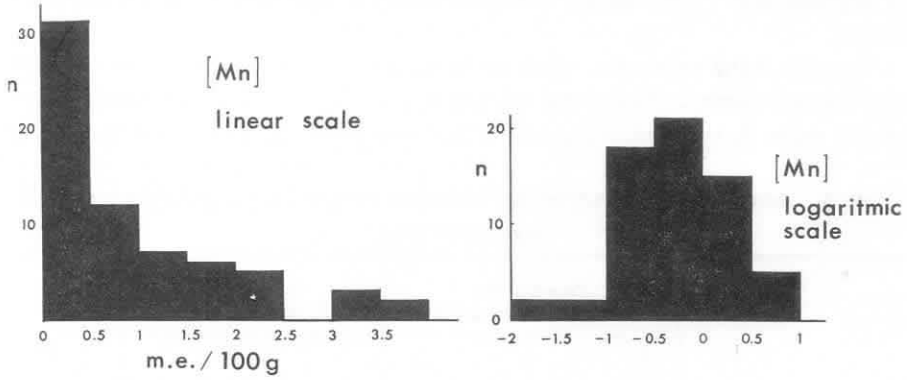

Fig. 2. Frequency distribution of manganese in the entire set of samples on a linear and on a logarithmic scale.

Fig. 2 gives as an example the frequency distribution of concentration of manganese in the entire set of samples on a linear and on a logarithmic scale. It is seen that the distribution on a linear scale is highly skewed, while the distribution on a logarithmic scale is more normal. Similar features were observed with respect to other cations. For this reason all concentrations of cations were transferred to logarithmic values in the statistical analysis.

Based on these considerations the following 8 variables were included in the statistical analysis.

1. Loss on ignition (I %)
2. Nitrogen taken as per cent of loss on ignition (N %).
3. Logarithmic value of calcium concentration (Ca).
4. ,, ,, ,, magnesium ,, (Mg)
5. ,, ,, ,, manganese ,, (Mn)
6. ,, ,, ,, sodium ,, (Na)
7. ,, ,, ,, potassium ,, (K)
8. Base saturation percentage (B %).

2. *Analysis of variance*

As an initial step an analysis of variance was carried out. The variance of each variable within and between types were calculated and the corresponding F-ratio, as well as the mean of each variable within each type. The results are presented in table 3. Where logarithmic variables were used, the figures given in tab. 3 are the linear values corresponding to the logarithmic means. With 8 and 55 degrees of freedom all F-values are significant, for Ca at the 1 per cent level, the rest at the 0.1 per cent level. It is immediately evident that the grouping of vegetation in types contain a large amount of information about soil properties.

In table 3 the vegetation types are arranged in an approximate series with oligotrophic communities to the left and eutrophic or calcicolous communities to the right. A systematic pattern of soil properties is seen. Thus there is a

Table 3. *Analysis of variance of soil chemical properties stratified according to vegetation type.*

	Pine forests *Cladonio-Vaccinietalia*				Spruce forests *Vaccinio-Piceetalia*				F
	1 Vu– Pn	2 Cl– Pn	3 Ba– Pn	4 Va– Pn	5 Eu– Pc My	6 Eu– Pc Dr	7 Me– Pc ty	8 Me– Pc At	
	Number of samples								
	6	6	9	4	10	10	10	9	
Loss on ignition (I%)	96,0	89,9	78,9	79,1	64,5	32,6	25,3	33,4	29,6
Nitrogen percent (N%)	1,33	1,42	1,60	1,47	1,93	2,14	2,09	2,84	27,0
Ca me/100 g	8,9	12,0	6,1	15,2	8,2	5,3	5,0	19,6	3,22
Mg me/100 g	3,95	2,56	2,33	2,33	1,47	0,82	0,63	1,40	7,83
Mn me/100 g	0,27	0,20	0,23	1,52	0,41	0,62	1,55	0,89	4,38
Na me/100 g	0,50	0,45	0,31	0,13	0,11	0,08	0,06	0,11	17,9
K me/100 g	1,98	1,30	1,80	2,02	1,17	0,58	0,33	0,41	10,3
Base saturation (B%)	13.8	14.0	12,7	20.6	13,7	23,9	28,2	44,6	15,9

systematic increase in N %, Mn and B % from oligotrophic to eutrophic communities, while the inverse is true for I %, Mg and Na.

Since there are evident correlations between the chemical properties of the soils it cannot be concluded that each factor showing a high F-ratio is an important factor determining the composition of the plant communities. Thus the F-ratio for Na comes out very high (17.9). It is seen that Na varies approximately inversely with base saturation (B %). A high base saturation is associated with a high population of divalent ions absorbed on the colloids which affects the binding of Na to the colloids. Thus Na is not so firmly bound to the colloids if base saturation is high and therefore more easily washed out. Manganese varies with base saturation. Low base saturation is followed by low pH and in an acid environment with humus, manganese is mobilized as divalent ions and leached out.

Since several soil properties are intercorrelated, it is difficult to conclude from the analysis of variance whether a certain factor, considered apart from the other intercorrellated factors, contributes to the difference between the vegetation types. The statistical tool available for a more refined analysis of such problems is discriminant analysis.

3. *Discriminant analysis*

The principles of discriminant analysis was first suggested by FISHER (1936) and has later been elaborated by others (RAO 1952, BARTLETT 1965). Suppose there are two different populations and for each member of each population p different measurements are made. Now a new variate is made.

$$z = b_1x_1 + b_2x_2 + \dots b_px_p$$

where x_1, x_2 .... x_p are values of measurements and b_1, b_2 .... b_p are constants. For any chosen set of the constants a value of z for each member of each population is obtained. From this the mean values of z within each population, their difference and its standard error and the significance of the difference can be calculated. Now the values of the constants b_1, b_2 .... b_p are determined in a way to make the statistical significance as high as possible. This means maximising the ratio of the difference to its standard error by variation of the constants b_1, b_2 .... b_p. The difference between the means of z of the two populations thus obtained is signified by the letter D. It is a measure of the difference between the populations in terms of the variables included in the analysis. The projection of the point clusters in fig. 1 on an axis parallel the regression line represents a crude form of discriminant analysis.

For a complete analysis each type must be compared with all other types, with 8 vegetation types altogether 28 comparisons.

A standard IBM program for stepwise discriminant analysis was used, based on a method in analogy with partial regression analysis first suggested by FISHER (1936 pp. 184—185). We are indebted to the staff of the Computing Centre at the Agricultural College of Norway for help with the calculations. In each comparison the sums of products of 8 variables within each type are calculated and added giving an 8 × 8 matrix of sums of products. The matrix is inverted and from this the values of the b's, the contribution to the total sum of squares due to each variable, the value of D and its significance are calculated. A comparison of the sum of squares due to each variable with the error mean square gives the significance of each b.

When the first analysis is carried out, the variable contributing the least sum of squares to the total is deleted, leaving 7 variables. The program is now repeated with 7 variables, and the variable now contributing the least sum of squares deleted, leaving 6 variables. The program is repeated until only one variable is left.

An example of the results of such an analysis comparing the *Eu-Piceetum Dryopteris* subassociation with the *Myrtillus* subassociation is given below. * means significance at the 5 per cent level, ** significance at the 1 per cent level and *** significance at the 0.1 per cent level.

Number of variables included	D	Element to be removed	Significant elements
8	0,934**	Mg	— I%*
7	0,934**	N%	— I%**
6	0,933***	K	— I%**
5	0,923***	Mn	— I%***, + B%*
4	0,893***	Na	— I%***, + B%*
3	0,848***	Ca	— I%***, + B%**, + Ca*
2	0,536***	B%	— I%***, + B%***
1	0,177***	I%	— I%***

The features of this comparison is typical of many in the material. It is seen that when the first 3 variables are removed the value of D drops from 0.934 to 0.923 suggesting that Mg, N % and N contribute but little to the difference between the types. In spite of the data presented before, suggesting significant differences in N % between the types, the discriminant analysis suggests that this difference can be accounted for by intercorrelation between N % and other variables.

Removal of unnecessary variables increase the significance of D and the remaining b's. When the last 3 variables Ca, B % and I % are removed the value of D drops sharply suggesting that these are important discriminators.

This is also borne out by an examination of the significance of the elements considered separately.

From the comparison it is concluded that significant differences in chemical soil factors between the types exist. The *Dryopteris* subassociation has a significantly lower loss on ignition but on the other hand a higher base saturation than the *Myrtillus* subassociation. There is also some slight evidence that the amount of Ca is higher in *Dryopteris* subassociation considered apart from the contribution of Ca to the base saturation.

Table 4. *Ecological distance between the vegetation types in terms of measured soil properties. Upper right values of D, lower left their statistical significance, Further explanation in text.*

Type	Pine forests *Cladonio-Vaccinietalia*				Spruce forests *Vaccinio-Piceetalia*			
	1 Vu–Pn	2 Cl–Pn	3 Ba–Pn	4 Va–Pn	5 Eu–Pc My	6 Eu–Pc Dr	7 Me–Pc ty	8 Me–Pc At
1 Vu–Pn		1,15	2,27	21,7	2,43	11,71	9,45	24,80
2 Cl–Pn	n.s.		2,29	123,7	1,41	7,63	9,16	8,90
3 Ba–Pn	*	n.s.		0,58	1,01	2,05	3,32	11,70
4 Va–Pn	n.s.	*	n.s.		0,90	10,2	19,8	21,6
5 Eu–Pc My	**	*	**	n.s.		0,93	0,85	2,00
6 Eu–Pc Dr	***	***	***	**	**		0,21	0,93
7 Me–Pc ty	***	***	***	***	**	n.s.		1,79
8 Me-Pc At	***	***	***	**	***	**	***	

A Comparison of the Ecological and Floristic Differences between the Vegetation Types

In table 4 the values of D are given together with their significance. Between the pine forest types the significances are slight or absent suggesting no significant difference between the types in terms of the soil factors measured. There are other differences, thus the *Vaccinio uliginosi-Pinetum* grows on thick peat while the others grow on mineral soils, but the chemical properties of the humus seem not to be very different. It will be seen that high values of D are encountered in comparisons where the *Vaccinio-Pinetum* is involved but their significance may be low. Of the *Vaccinio-Pinetum* only 4 soils samples were available. In the comparison with the *Cladonio-Pinetum* with 7 soil samples there are only 2 degrees of freedom left for D and an erratic behaviour of D is to be expected. This may serve as a warning not to use too few samples in such comparisons.

Within the spruce forest types there is no significant difference between the *Eu-Piceetum Dryopteris* subassociation and the *Melico-Piceetum* typical subassociation. The two types, when occurring in the same district tend to grow on different exposures, the *Melico-Piceetum typicum* on southfacing slopes, while the *Eu-Piceetum Dryopteris* subassociation tends to grow on northfacing slopes.

The *Melico-Piceetum Athyrium* subassociation seems, ecologically speaking, to be different from all the other types.

Comparing spruce and pine forest types significant or highly significant differences are found in all cases except one, in the comparison between the *Vaccinio-Pinetum* and the *Eu-Piceetum Myrtillus* subassociation. The *Vaccinio-Pinetum* is the pine forest type most closely related to the spruce forests (see p. 516).

A comparison of table 2 and of table 4 is of interest since the index of floristic community is considered a measure of floristic similarity. If the chemical soil factors are determinants of floristic composition, a correspondence between the data in table 2 and table 4 is to be expected. There is also a general correspondence between the values of D and their significance and the Sørensen indices on the other hand, low values of the indices corresponding to high values of D and high significance.

D is the measure of the difference between populations in terms of the measured variables known as Mahalanobis generalized distance. However, as BARTLETT (1965) points out, it is not an Euclidian distance in multidimensional space. If the variables are measured in milliequivalents the dimension of D is milliequivalents^2. For this reason the square root of D is considered a more appropriate measure of distance between the populations.

The Sørensen index of floristic community measures similarity in floristic composition between the populations and varies between 1 and 0 or in per cent 100 and 0. If two communities are entirely different the value of the index is 0. For this reason it seems better to use $1/K_s$ as a measure of difference between populations.

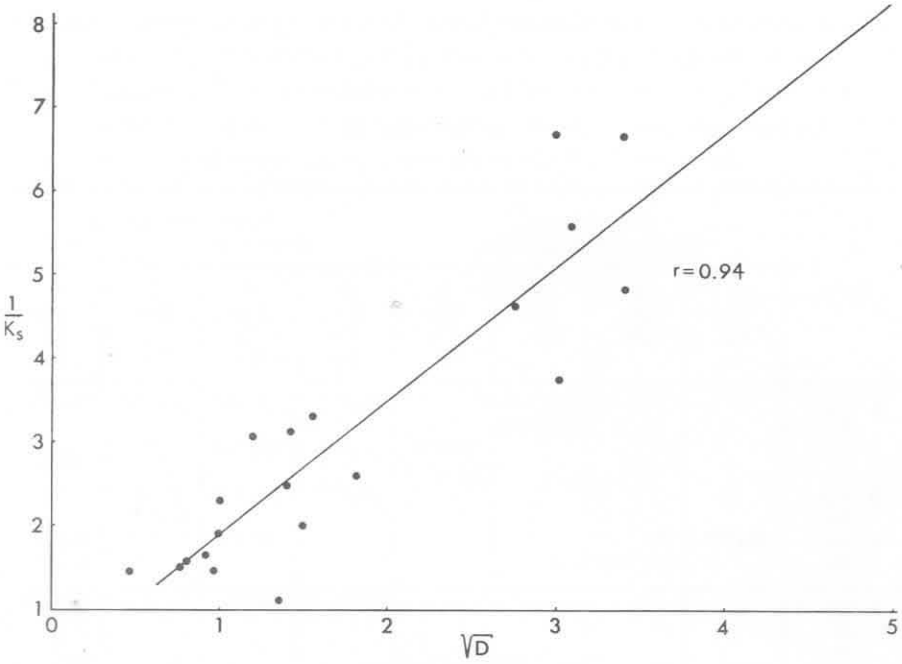

Fig. 3. Relationships between the measures of floristic distance ($1/K_s$) and ecological differcence ($\sqrt{D}$) for the different vegetation types. Further explanation in text.

In fig. 3 the values of $1/K_s$ is plotted against the square root of D with 6 or more degrees of freedom of D. A too high correlation is not to be expected since climatic factors and soil chemical factors other than those measured also determine floristic composition. In spite of this a good linear correlation of 0.94 is obtained.

Thus there is a fair amount of correspondence between the grouping of the vegetation types according to floristic composition and the chemical properties of the humus. Indeed K_s in this case seems to be a fair measure of the ecological difference between the types in terms of soil chemical factors.

Vegetation Types in Relation to Soil Chemical Factors

As pointed out the discriminant analysis also gives information about the individual factors significantly contributing to the difference between the types compared.

Table 5. *Differences in chemical soil factors between vegetation types as revealed by discriminant analysis. Vegetation types indicated by horizontal rows are positive in terms of factors in relation to types indicated by vertical columns. ** means significance at 1 % level, *** significance at 0.1 % level. Further explanation in text.*

Type	Pine forests *Cladonio-Vaccinietalia*				Spruce forests *Vaccinio-Piceetalia*			
	1 Vu– Pn	2 Cl– Pn	3 Ba– Pn	4 Va– Pn	5 Eu– Pc My	6 Eu– Pc Dr	7 Me– Pc ty	8 Me- Pc At
1 Vu– Pn			I%*** B%***		Na***	I%***	Mg***	Na***
2 Cl– Pn				Na*** N%***	Na***	I%***	Ca***	Mg***
3 Ba– Pn					Na***	I%***	I%*** K***	I%**
4 Va– Pn	Mn***	I%** B%**				I%***	Ca***	Mg*** Mn**
5 Eu– Pc My			Ca**			I%***	Ca***	I%***
6 Eu– Pc Dr	K***	K*** N%**	N%***	N%*** K**	B%***			
7 Me– Pc ty	Mn***	B%***		B%***	B%***	N%***		
8 Me– Pc At	N%***	N%***	N%***	N%***	Ca***	N%***	N%***	

In table 5 the results of this analysis are given based on the methods outlined before. The most significant differences are found when 3 or 4 variables are left in the analysis, i.e. when the unnecessary factors are left out while the more significant factors are included. By following along the horizontal row of a type (table 5) the data tell in which chemical property the type differs from others in the positive sense i.e. where the type has higher values for the chemical factors than the types indicated by the columns. Conversely by following a vertical column it is seen in which chemical factors the type differs from other types in a negative sense.

Comparing pine and spruce forest types it is seen that in general the spruce forest types have a higher N % and B % while on the other side the pine types have a higher I % and more of Na and Mg. Some apparent peculiarities are present. Comparing the *Cladonio-Pinetum* with the *Melico-Piceetum typicum,* the former have a higher amount of Ca while the latter has a higher base saturation. Similar features are evident in three comparisons where the *Melico-Piceetum typicum* is involved. This means that if the effect of base saturation is accounted for, the *Melico-Piceetum* is low in Ca i.e. that other ions contribute relatively more to the base saturation than Ca in the *Melico-Piceetum* typicum.

Within the pine forests the differences are small, as also indicated by D in table 5. The many significant differences between the *Cladonio-Pinetum* and the *Vaccinio-Pinetum* should be taken with some reserve, because of the relatively few samples in this comparison. The *Vaccinio uliginosi-Pinetum* is low in Mn in relation to the *Vaccinio-Pinetum* and also in relation to the *Melico-Piceetum typicum*. This is reasonable since the *Vaccinio uliginosi-Pinetum* grows on ombrogenous bogs.

Within the spruce forest types the differences seem to be mainly in nitrogen and base saturation while the *Eu-Piceetum* has a higher loss on ignition than the *Melico-Piceetum*.

In fig. 4 the nitrogen percentage is plotted against base saturation with different symbols for each vegetation type in the same way as in fig. 1. Apart from the *Vaccinio-Pinetum* the pine forest types have been taken together since the discriminant analysis reveals only little difference between the pine forest types. The general picture of fig. 1 is repeated in fig. 4. The *Melico-Piceetum Athyrium* subassociation has the highest N % and B %, then follows the *Melico-Piceetum* typical subassociation and the *Eu-Piceetum Dryopteris* subassociation which occupy approximately the same field. The *Eu-Piceetum Myrtillus* subassociation tend either to have a lower base saturation or a lower nitrogen percentage, but still higher than the pine forest types. The picture in fig. 4 is a little more complicated than in fig. 1, this is probably due to the fact that the samples come from a wider geographical area. As in fig. 1 there is a significant positive correlation between base saturation and nitrogen.

From the analysis it can be concluded that the content of nitrogen, the base saturation and the content of organic matter in the humus layer are the most important factors discriminating between the vegetation types. But also other factors such as the amounts of Ca, Mg, Mn, N and Na are of importance in some cases.

Discussion

The supply of cations depends upon the parent material and the weathering and leaching of the soil as well as supply from precipitation. These ecological factors can be classified according to FRIES (1925) as primary environmental

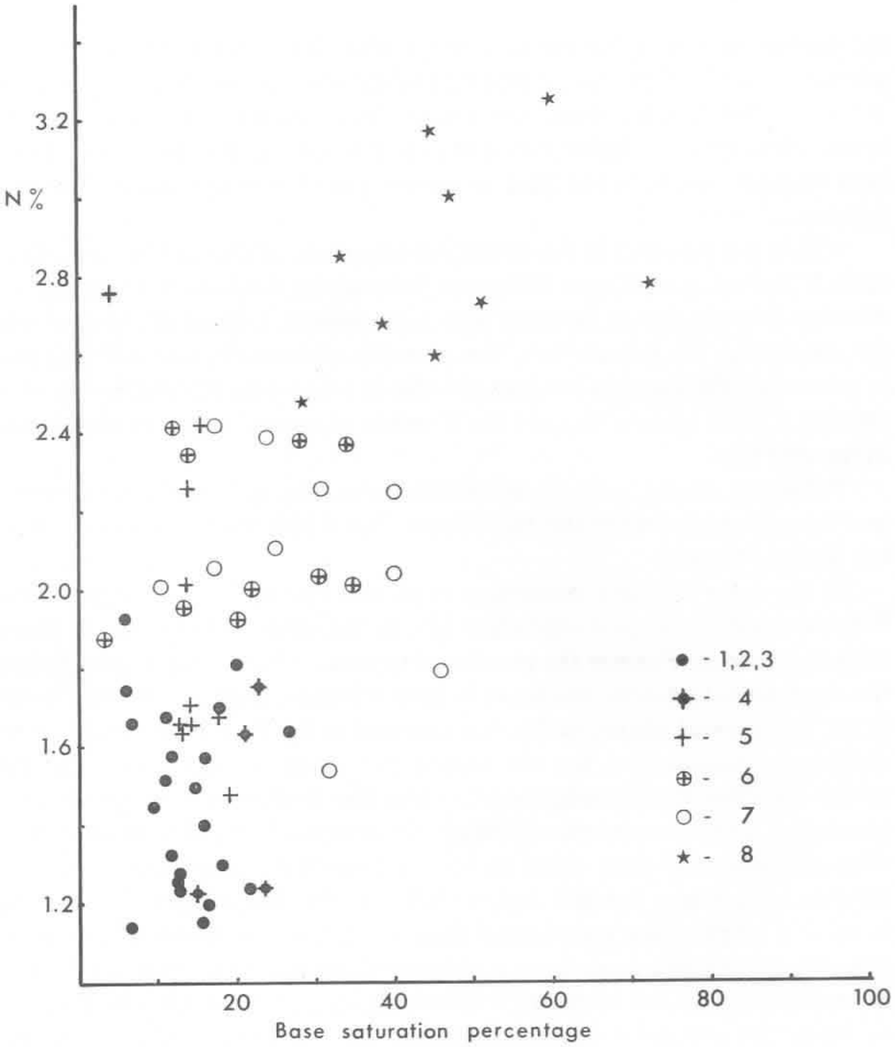

Fig. 4. Nitrogen percentage plotted against base saturation for the entire set of samples. 1) Vu-Pn, 2) Cl-Pn, 3) Ba-Pn, 4) Va-Pn, 5) Eu-Pc My, 6) Eu-Pc Dr, 7) Me-Pc ty and 8) Me-Pc At.

factors or following MARR (1961 p. 9) they are external environmental factors. On the other hand the amount of organic matter in the humus layer and the content of nitrogen in the humus are results of the processes in the ecosystem. In the terminology of FRIES they are secondary environmental factors or following MARR they are internal environmental factors. Base saturation occupies a position between primary and secondary environmental factors.

Despite the fact that the division line not always is sharp, the distinction between primary and secondary environmental factors is important in any discussion about causal relationships between environment and vegetation. A primary or external environmental factor can be a determinant of the composition of the ecosystem and its geographical distribution and local occurrence, while the same is not the case for secondary or internal environmental factors.

The amount of humus in the A_0 og A_1 layers depends *inter alia* on the activities of the earthworms and other animals in the soil and on transport of minerals by water movements. In the well-drained and acid soils in the pine and oligotrophic spruce communities no important mixing of humus and mineral material takes place, and the humus layer is low in mineral material.

The amount of nitrogen in the humus layer is of particular interest. The low nitrogen content in pine forest humus as compared with spruce forest humus might be due to differences in the litter produced in these forest types. It is known that different species differ in the chemical composition of the litter, thus birch and spruce forest litter tends to be higher in nitrogen than pine forest litter (MORK 1942, AALTONEN 1948 p. 153 ff., BONNEVIE-SVENDSEN and GJEMS 1957). The chemical composition of the litter also varies with environmental factors. But differences in nitrogen percentage in the humus migth also be due to differences in the environmental conditions for animal and microbial activity resulting in different paths of breakdown of the litter.

A multiple correlation analysis between nitrogen percentage of the humus and the other soil chemical factors was carried out and resulted in a multiple correlation coefficient of 0.95. This good correlation does not help much. The explanation might be that pine occupies the poorest sites and for this reason a correlation between other chemical soil factors and nitrogen percentage is found.

A suitable situation for deciding between the alternatives would be a locality with natural pine forests growing on soils normally occupied by spruce. Such a situation exists on the island of Langøy near Langesund on the coast of South Norway on limestones and schists. Here spruce is lacking except for a few individuals. The reason for the absence of spruce is not clear, but may be due to difficulties in the establishment of the seedlings. Pine forests are found on deep soils with a brown earth profile and with an associated flora with many species absent from oligotrophic pine forest but present in calcicolous spruce forests. The vegetation has been studied by mr. Marker, University of Oslo, who also collected soil samples. The samples were analyzed at the Norwegian Forest Research Institute by the same methods as outlined before. We are very grateful to mr. Marker for permission to use his data.

The most widespread pine forest type have *Calamagrostis epigeios* and *Convallaria majalis* as dominant species in the field layer. The mean nitrogen percentage of the humus of the A_1 layer is 2.47 with a standard error of 0.75 based on 12 samples. This figure is not different from that found in eutrophic and calcicolous spruce forest types (see table 3). Thus the difference in nitrogen cannot be due to the dominant tree but is more likely to depend on soil conditions or possibly ground vegetation.

It has been noted that also within the spruce forest types there are significant differences in nitrogen percentage of the humus. HESSELMAN (1926 p. 303) showed that the nitrogen percentage in the humus of conifer forests decreased with increasing loss on ignition and increased with increasing pH. A similar situation also exists in mires (HOLMEN 1964) with increasing nitrogen content from the most oligotrophic to the most eutrophic vegetation types.

The results suggest that the nitrogen content of the humus depends upon some primary or external environmental factor primarily acting on the breakdown of the litter in the soil. The analysis also suggests that the differences in nitrogen are associated with differences in base saturation.

A high base saturation is associated with a supply of metal cations to the ecosystem, especially calcium ions. Thus the supply of calcium from the parent soil may be the primary ecological factor responsible for the differences in nitrogen content of the humus.

This result may also be of interest regarding the supply of nutrients for forest growth. The series from oligotrophic forest types is associated with differences in forest productivity.

From fertilization experiments it is known that nitrogen is a limiting factor of growth. A supply of nitrogen dramatically increases growth the first few years, then growth decreases with time to normal values (see e.g. TAMM and CARBONNIER 1961, MORK and BRANTSEG 1963). After a time the added nitrogen is incorporated in the ecosystem. Since the nitrogen turnover in northern forests is slow and the amount of nitrogen added by fertilization is small in comparison with the nitrogen capital of the ecosystem, a long-term effect of nitrogen fertilization is hardly to be expected. It is also known that a high nitrogen percentage in the humus is associated with a good supply of nitrogen for forest growth. Thus the higher productivity in calcicolous and eutrophic forest types might be due to differences in the supply of nitrogen.

It is also known that differences in amounts of calcium in the soils is associated with differences in forest growth. Thus DAHL, SELMER-ANDERSSEN and SÆTHER (1961) found that about half the variance in growth of pine forest types in Finland analyzed by VIRO (1955) could be explained from the available calcium. Liming of acid forest types has long been used as a mean of increasing forest growth. Fertilization by calcium seems to result in a low increase in growth which, however, lasts long.

It seems, however, unlikely that the amount of available calcium as a plant nutrient limits growth. Thus Wallace, Frolich and Lunt (1966) showed that the need of calcium in carefully balanced medium is very low, and it is very unlikely that this amount of calcium is not available even in very nutrient-poor soils. It is possible that the effect of liming in forests is mediated by the effect of a higher base saturation on the nitrogen turnover. This might explain the slow response of tree growth on liming as well as its long duration.

Concluding remarks

The picture emerging from this analysis seems to be that the supply of divalent ions, especially calcium ions, from the soils is a primary or external environmental factor responsible for the differentiation of several conifer forest types. This primary or external factor acts in part through nitrogen turnover in the humus layer thereby affecting the supply of available nitrogen for forest growth. In this way differences in productivity of the types might be explained.

It must be emphasized that this should be taken as a working hypothesis. Experiments with fertilization and liming stratified according to vegetation types and further studies on microbial and animal turnover of nitrogen in the different forest types might help to clarify the problems.

It seems surprising with the limited number of samples available that so many significant differences in soil chemical factors between vegetation types could be found. The explanation is likely to be that samples were only collected in typical stands belonging to defined sociological types. This reduces variation within types with a better chance of detecting differences between types. This suggests that a pre-stratification of samples according to plant sociological characters of vegetation is helpful in an analysis of ecological relationships of vegetation.

Vegetasjonstyper i norske barskoger i forhold til humuslagets kjemiske egenskaper

I dette arbeide fremlegges resultatet av en undersøkelse over sammenhengen mellom humussjiktets kjemiske egenskaper i forskjellige vegetasjonstyper i barskog på Østlandet. Det ble samlet prøver fra følgende skogsamfunn, 1) furumyrskog, 2) røsslyngfuruskog, 3) lavfuruskog, 4) bærlyngfuruskog, 5) blåbærgranskog, 6) småbregnegranskog, 7) lågurtgranskog og 8) høgstaudegranskog. De undersøkte kjemiske faktorer var, 1) glødetap, 2) nitrogen (prosent av glødetap,) 3) calsium, 4) magnesium, 5) mangan, 6) natrium, 7) kalium og 8) basemetningsgrad.

En orienterende variansanalyse viste at det for alle undersøkte faktorer var sikre statistiske forskjeller mellom typene. Ved hjelp av en diskrimansanalyse ble det så undersøkt hvilke vegetasjonstyper som var sikkert forskjellige, og hvilke faktorer som bidro til denne forskjell — uavhengig av samvariasjon mellom faktorene. Nitrogeninnhold, basemetningsgrad og glødetap var de viktigste diskriminerende faktorer og mellom de fleste av vegetasjonstypene var humusegenskapene statistisk forskjellige. Det viste seg også at det var en god sammenheng mellom vegetasjonstypenes floristiske slektskap og likhet i humusegenskaper. Mellom enkelte nærstående typer hvor de økologiske forskjeller var små er det trolig andre faktorer enn de undersøkte, f.eks. høydelag eller substrattype som skiller mellom typene.

Humuslagets nitrogeninnhold synes å være en særskilt viktig faktor som skiller furu- og granskogsamfunn, og som også skiller mellom de forskjellige granskogsamfunn. Da nitrogeninnholdet er en sekundær vekstfaktor (avhengig av prosesser i skogsystemet), må dette igjen være avhengig av primære dvs. opprinnelige vekstfaktorer. Basemetningsgrad er sterkt positivt korrelert med nitrogeninnholdet. Innholdet av toverdige katjoner, særlig av kalsium er da antagelig primære vekstfaktorer av betydning for humuslagets nitrogeninnhold og for differensieringen av enkelte skogsamfunn. Disse faktorer virker også inn på nitrogenomsetningen og derigjennom på trærnes vekst, og kan delvis forklare forskjellen i produksjonsevne mellom de forskjellige skogsamfunn.

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